



Dating North Asian surface assemblages with ostrich eggshell: implications for palaeoecology and extirpation

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ABSTRACT

East Asian ostrich (*Struthio anderssoni* Lowe) was thought to have become extinct sometime in the Late Pleistocene. Petroglyphs portray ostrich with Pleistocene animals, and ostrich eggshell (OES) fragments and ornaments from Holocene sites were considered to be older fossils. Here we summarize previous radiometric dates for ostrich eggshell (OES) and present 15 new calibrated accelerator mass spectrometry (AMS) dates, indicating that ostrich survived in Mongolia and northern China until at least 8.9 ka BP. The dates in our sample population suggest a correlation between *Struthio* and warm steppe environments, with extirpation probably related to essential changes in Holocene steppe ecosystems including human expansion. This study assesses the usefulness of Asian OES for archaeological dating by AMS, constrains the date of Asian ostrich extirpation, and investigates palaeoenvironmental implications of ostrich survival and extinction.

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1. Introduction

Ostrich (*Struthio* sp.) was a component of North Asian fauna as early as the Miocene (Andersson, 1923; Lowe, 1931; Bibi et al., 2006), but is mostly known from ostrich eggshell (OES) fragments and beads from archaeological sites between trans-Baikal Siberia and northern China (Fig. 1) (Lowe, 1931; Maringer, 1950; Aigner, 1981; Derevianko, 1998; Jaubert et al., 2004; Xia et al., 2001; Zhang, 2001; Martynovich, 2002; Mei, 2007). In northern China Pleistocene faunas, *Struthio* co-occurs with other desert, arid-steppe and grassland species such as *Equus przewalski*, *E. hemionus*, *Gazella subgutturosa*, and *Microtus brandtoidies* (Deng, 2006), as well as *Elephas*, *Coelondonta antiquitatis*, *Megaloceros ordosianus*, *Bos primigenius*, *Crocota crocota ultima*, and *Ovis ammon* (Lowe, 1931; Aigner, 1981). Ostrich-like birds are depicted in rock art of the Chinese Helan Shan and Yin Shan (Gai, 1989; Xu and Zhong, 1993), and Mongolian Altai in association with rhinoceros, horse, aurochs, and humans (Tseveendorj et al., 2005).

Mammuthus and *Struthio* appear to have been the last Asian Pleistocene “megafauna” to become extinct. Radiometric dates

from North Asian archaeological deposits containing OES (associated dates) extend the possible temporal range for *Struthio* to the terminal Pleistocene (Table 1). Heretofore, the few direct dates on OES were late in Marine Isotope Stage (MIS) 3 (60–25 ka BP) (Table 1) (Madsen et al., 2001; Jaubert et al., 2004). While some archaeologists suspected that ostrich survived as late as the Holocene, direct evidence was lacking.

Microlithic surface sites in north China and Mongolia are abundant, and in addition to lithics, often contain OES fragments, decorated pieces and disc beads (Maringer, 1950; Fairservis, 1993; Bettinger et al., 1995; Elston et al., 2001; Janz, 2006). The use of OES for beads and water carriers and depictions of ostrich in petroglyphs or on ceramic vessels was common amongst hunter-gatherers and pastoralists, as evidenced in southern Africa (Butzer et al., 1979; Kandel and Conrad, 2005; Orton, 2008), northern Africa (Kryzaniak and Kroeper, 1985; VanNeer and Uerpmann, 1989; Friedman et al., 1999), the Arabian peninsula (Potts, 2001), and India (Badam, 2005). Ostrich also appears to have had held ideological significance in some desert cultures (Friedman et al., 1999; Potts, 2001).

Thought to date from the Late Pleistocene to Early Holocene, the exact chronology of microlithic sites in North Asia is unknown. Few sites have been excavated and most lack temporally sensitive artifact types, or organic remains like charcoal and bone. The use of direct AMS dates on OES offers the best opportunity for dating

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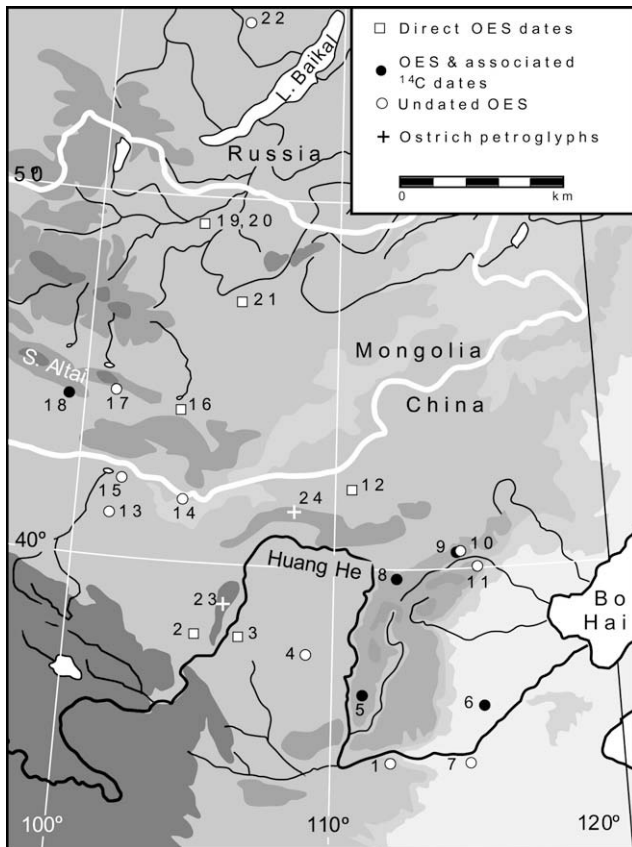


Fig. 1. Locations of north Asian archaeological sites containing *Struthio* OES or depictions of ostrich-like birds. Open squares are sites containing directly dated OES; closed circles are sites containing OES in association with dated archaeological sediment; open circles are undated microlithic surface sites with OES, or sites with OES in undated or poorly dated sediment; crosses are locations of ostrich-like petroglyphs. 1, Yangshao (Andersson, 1923); 2, Toudaohu (Elston et al., 2001); 3, Shuidonggou (Madsen et al., 2001); 4, Salawasu (Aigner, 1981); 5, Xueguan (Aigner, 1981; Zhang, 2001; Barton et al., 2007); 6, Xiaonanhai (Aigner, 1981; Zhang, 2001; Barton et al., 2007); 7, Lingching (Aigner, 1981); 8, Shiyu (Aigner, 1981; Zhang, 2001; Barton et al., 2007); 9, Hutouling (Aigner, 1981; Zhang, 2001; Barton et al., 2007); 10, Yujiagou (Xia et al., 2001; Zhang, 2001); 11, Zhoukoudian, Upper Cave (Aigner, 1981; Zhang, 2001; Barton et al., 2007); 12, Baron Shabaka (Fairservis, 1993); 13, Gurnai (Maringer, 1950); 14, Yingen-Kuduk (Maringer, 1950); 15, Sogho-nor (Maringer, 1950); 16, Shabarakh-usu (Fairservis, 1993; Janz, 2006); 17, Tsagaan Agui (Martynovich, 2002); 18, Chikhen Agui (Derevianko et al., 2003); 19, Dörölj 1 (Jaubert et al., 2004); 20, Ulan Ereg; 21, Baga Gazaryn Chuluu; 22, Krasny Yar (Derevianko, 1998); 23, Helan Shan (Xu and Zhong, 1993); 24, Yin Shan (Gai, 1989).

these assemblages, although the direct association of AMS dates from OES artifacts is problematic since OES persists in landscapes (Potts, 2001). Inhabitants of the Gobi Desert appear to have occasionally used fossil material for ornaments (Aseyev, 2008). A solution to the old-shell problem is to date multiple samples of OES from the same site to obtain a statistically meaningful sample population. If the OES dates are consistent in a particular site one may provisionally conclude that the lithics and OES are contemporary. Similar dates from multiple related sites increase confidence in the results.

2. Methods

2.1. Sample selection

We chose OES samples from as wide a geographic range as possible in northern China and Mongolia (Fig. 1). Mongolian

samples include ten items from microlithic-dominated Shabarakh-usu (Bayan-dzak) localities 2 and 7. Both are from Gobi Desert Mesolithic-to-Neolithic transition type sites, collected during the 1925 Central Asiatic Expedition, American Museum of Natural History (AMNH) (Chard, 1974; Fairservis, 1993; Janz, 2006). AMNH samples 73-790-01, -02, and -03 (AA76416 to AA7618) were unworked and are from an excavated section of locality 2 that was not associated with OES beads. Samples 73-764-01 (AA76419) and 73-1035-01 (AA76425) were bead-blanks or preforms (OES fragment worked into a circular shape, but lacking drilled hole in center) that conform to Orton's (2008) Pathway 2 mode of production for the South African Later Stone Age. The remaining samples from the Shabarakh-usu group were associated with drilled OES beads of both the angular and circular types, suggesting two different production strategies: (1) drilling of angular fragment before final forming, and (2) rounding of angular fragment before drilling (Orton, 2008).

Two additional samples were collected in Mongolia during recent surveys conducted by Chunag Amartushvin, William Honeychurch and Joshua Wright. One of these specimens (AA80245), unworked but associated with evidence of bead-making activities, was found at the Ulan Ereg site (EGS 028) in a deflated Pleistocene dune in the Egiin Gol valley (very near Dörölj 1—see Fig. 1), which yielded over 1500 microliths, OES beads and bead preforms (Wright, 2006). The other specimen (AA80246), also unworked, is from BGC 1451, a site excavated from an outwash cut at Baga Gazaryn Chuluu, Middle Gobi, where the excavated cultural deposit directly overlay a layer of pale Pleistocene loess.

From Inner Mongolia are two unworked samples (73-2225-01/AA76426 and 73-2225-02/AA76427) from a group of 140 fragments associated with two OES beads. These were collected by the Central Asiatic Expedition in 1928 from the Mesolithic/ Neolithic Baron Shabaka Well site (BS 19) (Fairservis, 1993). One unworked specimen (Beta 132987) collected by the US/China Working Group on Late Quaternary Human Adaptation and Climate Change is from a small microlithic and ceramic surface assemblage in the Toudaohu Basin (TDH4) of the western Tengger Desert (Elston et al., 2001).

2.2. Sample processing

A number of published studies demonstrate the reliability of OES radiocarbon dates (Freundlich et al., 1989; Vogel et al., 2001; Bird et al., 2003). Samples measured at the University of Arizona (AA76416–AA76427, AA80245–AA80246) in July 2007 were subjected to a selective dissolution procedure designed to remove the outer layer of carbonate, to avoid potential contamination (Burr et al., 1992). In all cases, at least 50% of the sample was dissolved, and only carbonate from the interior was collected for measurement. This is the same procedure successfully applied to ratite eggshell samples from Australia by Bird et al. (2003). We measured the radiocarbon content of successively dissolved eggshell fractions for sample number AA76419 (AMNH 73-764-01) to assess possible post-depositional carbon exchange. The three values obtained for that sample agree at the 2σ level, and are therefore statistically indistinguishable, suggesting that OES is relatively inert and should provide reliable results (Table 2). A weighted average value of 7969 ± 37 was computed from the three results. The sample measured at Beta Analytic (Beta 132987) was combusted to release the carbon from the samples and not selectively dissolved. The results of Bird et al. (2003) compared the dissolution and combustion methods from the same samples, and suggest that either procedure should yield similar results. All ^{14}C dates reported here have been converted to calendrical dates with CalPal—2007 download (Weninger et al., 2009).

Table 1
Previously reported associated and direct archaeological dates for Pleistocene Asian *Struthio*.

Site	¹⁴ C age BP ± 1σ	Cal age BP ± 1σ/ka	Material	Lab. No.	References
Yujiagou		6.95 ± 0.35 ka 11.12 ± 0.89 ka	Quartz ^a Quartz ^a	UES-PKU 219 UES-PKU 221	Xia et al., 2001
Hutouliang	10689 ± 210	12530 ± 560	Fossil bone	PV0156	Aigner, 1981; Barton et al., 2007
Chikhen Agui, Hearth 4	11160 ± 160	13061 ± 176	Charcoal	SOAN3571	Derevianko et al., 2003
Xueguan	13167 ± 150	16220 ± 960	Charcoal	BK81016	Aigner, 1981; Barton et al., 2007
Xiaohanhui	23419 ± 500	28312 ± 1200	Charcoal	ZK-654	Aigner, 1981; Barton et al., 2007
Shuidonggou.	26930 ± 120	33232 ± 200	OES	Beta 132084	Madsen et al., 2001
Locality 2, Hearth 2	25670 ± 140	30874 ± 195	Charcoal	Beta 132083	
Shiyu	28135 ± 1330	33110 ± 2900	Bone	ZK-190-0	Aigner, 1981; Barton et al., 2007
Dörölj 1	29910 ± 310	34149 ± 276	Charcoal	GifA-99560	
	29540 ± 390	33822 ± 400	Charcoal	GifA-99561	Jaubert et al., 2004
	31880 ± 800	36368 ± 1218	OES	Gif-11664	
Krasny Yar	Older than 19000 ± 100	Older than 22867 ± 300	Bone	GIN-5330	Derevianko, 1998

^a Thermoluminescence date.

3. Results

New AMS dates on *Struthio* eggshell from six archaeological sites in Mongolia and northern China (Fig. 1) are given in Table 2. Specimens range in age from Middle MIS 3 (43.0 ka BP) to Early Holocene (8.9 ka BP). The oldest specimens are unworked fragments from Shabarakh-usu localities 2 and 7, TDH4 in the western Tengger Desert and from Ulan Ereg (EGS 028) in northern Mongolia. Association of these specimens with formalized microlithic assemblages indicates that fossil eggshell was either accidentally present or collected by later foragers. Evidence from the Gobi Desert for historic use of fossil eggshell is the recent find of OES engraved with the image of a ridden horse, stylistically consistent with Turkic period horseman images from the 6th to 8th century AD (Aseyev, 2008).

4. Dating archaeological surface assemblages using OES

Chronometric dates on OES have also been used in northern and southern Africa to infer the age of archaeological assemblages with minimal consideration of the old-eggshell problem (Freundlich et al., 1989; Vogel et al., 2001; Halkett et al., 2003). Eggshell for bead-making is thought to have been obtained from broken water carriers or through eggs collected for consumption (Sandelowsky, 1971; Orton, 2008), implying contemporaneity between OES and archaeological occupations. There are no known ethnographic examples of fossil eggshell use and no studies have yet been undertaken to test the relative quality of fresh over fossil eggshell.

Table 2
New AMS dates on ostrich eggshell from Mongolia and China.

Lab. No.	AMNH Cat. No. 73/	Site	δ ¹³ C	¹⁴ C age BP ± 1σ	Cal age BP ± 1σ
AA76416	790-01	SU2	-9.0	8396 ± 52	9401 ± 66
AA76417	790-02	SU2	-11.1	8268 ± 44	9268 ± 99
AA76418	790-03	SU2	-10.7	30490 ± 780	34049 ± 726
AA76419 ^a	764-01	SU2	-9.1	7969 ± 37	8852 ± 98
AA76420	763-01	SU2	-10.3	8159 ± 59	9134 ± 89
AA76421	763-02	SU2	-9.6	8184 ± 44	9145 ± 84
AA76422	1034-01	SU7	-11.3	8054 ± 43	8919 ± 96
AA76423	1034-02	SU7	-11.6	38600 ± 1000	43027 ± 823
AA76424	1034-03	SU7	-10.7	8439 ± 60	9458 ± 51
AA76425	1035-01	SU7	-11.0	8081 ± 49	8984 ± 96
AA76426	2225-01	BS19	-12.0	12509 ± 59	14829 ± 298
AA76427	2225-02	BS19	-10.7	12450 ± 74	14714 ± 333
Beta132987		TDH4	-11.9	33160 ± 180	37652 ± 640
AA80245		EGS028	-10.8	17100 ± 100	20456 ± 373
AA80246		BGC1451	-12.1	12203 ± 73	14255 ± 249

^a Weighted average of three dates from same shell fragment.

We suspect that fossil shell would be discoloured, much harder, brittle and more variable in thickness compared to fresh material. Incongruously old specimens in our sample did not display conclusive evidence of human modification, although the engraved Gobi Desert specimen (Aseyev, 2008) suggests that inferring the age of an archaeological site on the evidence of a singular AMS date could prove problematic.

The majority of AMS dates in these samples are consistent with the associated archaeological deposits. Two OES fragments from Baron Shabaka (BS 19), eastern Inner Mongolia, date to 14.8–14.7 ka BP and the specimen from the Mongolian Baga Gazaryn Chuluu site (BGC 1451) dates to 14.3 ka BP. These are well within the temporal range of microlithic technology. The tight cluster of eight OES dates between 9.5–8.9 ka BP from Shabarakh-usu localities 2 and 7 is consistent with the microlithic assemblages in which the OES specimens were found, suggesting human occupation and egg collection at both sites at about the same time in the Early Holocene.

The relatively large sample of similarly dated specimens from Shabarakh-usu localities suggests that despite the presence of fossils, the majority of OES are approximately the same age and probably coeval with human occupation. It is possible that the eight Early Holocene specimens were from old eggshells collected and discarded by even later people, but if so, we would not expect such a tight cluster of dates in a sample this large. Uniformity of AMS dates and consistency of associated archaeological assemblages suggests that occupation of Shabarakh-usu localities 2 and 7 probably date to between 9.5 and 8.9 ka BP.

5. Palaeoecological implications

While direct AMS dates on OES are important to the archaeology of the region, they are also significant to interpretations about the palaeoecology of North Asia during the Late Pleistocene, particularly since ostrich was one of few geographically dispersed Pleistocene megafauna to survive into the Holocene. While the earliest dates in this sample coincide with other evidence for the initial Upper Palaeolithic in Northeast Asia (Brantingham et al., 2001), the latest dates demonstrate the survival of *Struthio* in this region to the Early Holocene. Variation in abundance of dates through time seems to indicate sensitivity of Asian ostrich to Pleistocene climate change.

5.1. Palaeoclimate of monsoonal Central Asia

The region of North Asia considered here is part of monsoonal Central Asia where climate is largely determined by the relative

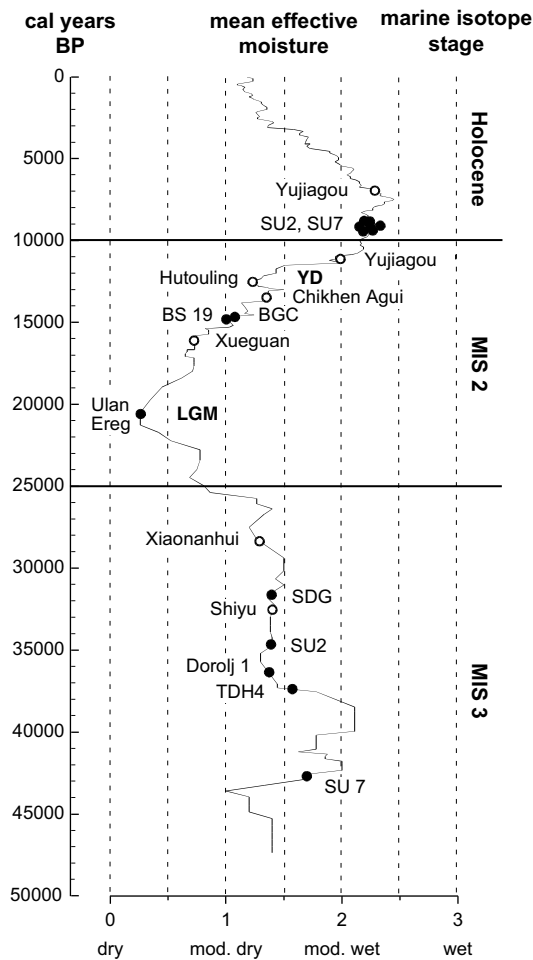


Fig. 2. Effective moisture curve for monsoonal central Asia. Plotted from data provided to the authors by U. Herzschuh, overlain with means of direct OES dates (closed circles) and dates of archaeological sediments containing OES (open circles).

strength of the winter and summer monsoons. When the Siberian–Mongolian high dominates, strong westerlies force the Indian and Southeast Asian monsoons south, blanketing the region with cold dry air in winter. When westerlies weaken, strong summer monsoons allow incursions of warm wet air into the region. The net result of monsoonal fluctuations in Central Asia have been expressed as a mean effective moisture curve by Herzschuh (2006) using a range of available palaeoclimate data for the region spanning the last 50 ka BP (Fig. 2). In order to facilitate a comparison between OES and palaeoclimate, this plot is combined with our direct and associated radiometric dates for OES (Tables 1 and 2) in Fig. 2.

5.2. Ostrich eggshell dates and climate change

OES dates from Toudaohu 4 and Shabarakh-usu 7 (AA76422) bracket the middle MIS 3 when climate was relatively warm and moderately wet to wet (Herzschuh, 2006). In the southern extent of our study area, large lakes occupied desert basins fed by glacial runoff from surrounding mountains. Mountain forests expanded, but desert vegetation dominated the lowlands (Herzschuh, 2006; Wünnemann et al., 2007). OES dates from Dörölj 1, Shabarakh-usu 2 (AA76418) and Shuidonggou, and associated archaeological dates from Shiyu and Xiaonanhu fall in late MIS 3 (37.6–25 ka BP), when climate was drier. Desert lakes persisted with brief periods of lower

water, and the Gobi was reduced by north and south extension of steppe forest and steppe (Feng, 2007). In early MIS 2 (25–19 ka BP), strong westerlies prevailed while the summer monsoons retreated, lake levels were medium-to-low and loess deposition increased (Wünnemann et al., 2007). At the LGM (21 ka BP), steppe and desert vegetation was shifted south to the Loess Plateau and eastward between 32°N and 40°N to the coast line; taiga extended far south into former desert steppe (Yu et al., 2000). The Ulan Ereg specimen from Egiin Gol valley in Bulgan province dates to this time (20.5 ka BP), but is the only direct or associated OES date between 22.6 and 15.3 ka BP.

Post-LGM climate (19.0–14.4 ka BP) somewhat ameliorated and lake levels were medium-to-high as steppe and forest steppe expanded (Wünnemann et al., 2007; Herzschuh and Liu, 2007). Overall moisture values for monsoonal Central Asia gradually increase to 17.2 ka BP, with stable to somewhat dryer values to 15.4 ka BP. A warming interval with a sharp increase in moisture between 15.4 and 13.0 ka BP coincides with OES dates from Baron Shabaka, Baga Gazaryn Chuluu and associated archeological dates from Xueguan and Chikhen Agui. Associated dates from Hutouling correspond with the Younger Dryas between 12.8 and 11.1 ka BP.

The cold dry Younger Dryas climate is followed by a continuing trend to warmer and wetter conditions through the Pleistocene/Holocene transition. The eight OES dates between 9.5 and 8.9 ka BP from Shabarakh-usu 2 and 7 occur near the end of this interval when standing water in the adjacent playa and surrounding desert steppe would have been an attractive habitat for both human foragers and grazing animals (Janz, 2006). Yujiagou contains OES in sediments dated by thermoluminescence (TL) to between about 11.1 and 6.9 ka BP (Xia et al., 2001), suggesting ostrich could have survived in northern China to the Mid-Holocene; however, the OES could be older than the enclosing sediments.

5.3. Ostrich metabolic requirements and climate

Wild ostriches in Africa (*Struthio camelus*) have similar dietary preferences to bovids and other grazing ruminants (Milton et al., 1994). Ostrich are highly selective, concentrating on a few green plant species of annual grasses and forbs that yield high protein, high fibre, and high calcium diets (Ullrey and Allen, 1996). While forbs and grasses are preferred, if unavailable, ostrich consume leaves, flowers and fruits, avoiding plants guarded by toxic substances (Milton et al., 1994). Offering an important seasonal boost in nutrients (Guthrie, 1984), forbs were likely important to East Asian *Struthio*.

Although African ostriches have a similar diet to ruminant grazers and compete with antelope in the wild, and with sheep and goats in domestic settings (Milton et al., 1994) they have some notable advantages over ungulates that may have helped Asian ostrich survive the LGM when other large herbivores did not. They have much higher reproductive rates and a life span in the wild of up to 40 years, which could mitigate unsuccessful breeding years. Ostriches can pull out and consume whole roots, allowing them to acquire nutrients from mature grasses and forbs (Williams et al., 1993). This may have helped ostriches, now present only in regions with less extreme seasonality, to cope with the shorter growing seasons of northern Asia (*sensu* Guthrie, 1984). Ostriches can cover long distances quickly and outrange most animals—wild ostriches in the Namib Desert are known to travel a minimum distance of between 7.7 and 18.5 km/day, with an average home range of 84.3 km (Williams et al., 1993). This should greatly increase the chance of locating scattered green foraging patches at washes and springs. Asian ostriches may also have been migratory like local species of gazelles (Schaller, 1998).

However, extremes in temperature and effective moisture can negatively impact population fitness. African ostriches obtain most moisture from their food and tolerate low temperatures, but drinking is important to sub-adults and newly hatched chicks are unable to thermoregulate (Brown and Prior, 1999). Industrial incubation studies indicate the importance of controlling necessary egg water loss and avoiding temperatures below 36 °C (Hassan et al., 2004). The larger size of *Struthio anderssoni* eggs compared to *S. camelus* (Lowe, 1931) suggests increased egg and body size as a cold adaptation. Additional cold weather physiological adaptations could have included increased fat storage and down, and better thermoregulation (unfortunately, such attributes are not preserved in eggshell, or skeletal remains, should those be found).

African ostrich breeding and egg laying depends on the synchronous occurrence of precipitation, warm summer temperatures and increased plant biomass; breeding occurs in wetter summer months only if there is enough rain to stimulate adequate vegetation growth (Williams et al., 1993). Thus, the MIS 2 (25–11.5 ka BP) climate, dominated by a strongly intensified winter monsoon with weakened summer monsoons and cold dry summers (Herzschuh, 2006) would have negatively impacted ostriches.

It would follow that while *Struthio anderssoni* tolerated a range of environmental conditions, it would have had greater reproductive success (reflected in numbers of eggshell dates) in arid North Asia during warmer moister intervals dominated by summer monsoons, and less success in cold dry intervals. Thus, *Struthio* population expansion could signal strengthening of the summer monsoons.

Although sample size is small, the distribution of direct OES and associated archaeological dates conforms to this expectation. Several dates occur in relatively warm and moist periods, but no direct dates occur in the cold dry first half of MIS 2 or the Younger Dryas. All derived from archaeological sites, these data may simply monitor human population dynamics, which at the LGM was drastically reduced above 42°N (Barton et al., 2007). But if *Struthio* was equally common in the LGM, we might expect several fossils of that age to occur in later sites. So far, however, the only LGM date is on OES specimen EGS 028 from Ulan Ereg at 49.5°N (Fig. 1), accompanying a microlithic industry that suggests fossil OES was associated with a later Pleistocene or Holocene occupation. Additional dates from a range of temporal and geographic contexts are needed to accurately assess the nature of a possible population depression during the LGM, but the current absence of LGM-aged OES further south indicates a shift in range of the species during a period of hyperaridity.

6. Possible causes for extinction of *Struthio anderssoni*

Considering the apparent adaptability of *Struthio*, the final Holocene extinction of the species in East Asia is surprising. As with the extinction of other large Pleistocene herbivores, the demise of ostrich in East Asia is an issue not easily resolved. Species that underwent significant range contractions or were wiped out entirely at the end of the Pleistocene are numerous and the phenomenon has stimulated fierce debate between those who believe that underlying shifts in climate and grassland ecology were responsible, and those who believe population increases and expansion of human predators was to blame. We propose that both climate and human population expansion were contributing factors and consider the individual role each may have played.

6.1. Holocene palaeoecology and ostrich vulnerability

Vulnerability of *Struthio* to perturbations associated with the unique climatic regime of North Asia are outlined above. Little is known about differences between the physiology of African and East

Asian ostriches, although the larger eggs of *Struthio anderssoni* suggest much larger body size (Lowe, 1931). East Asian ostriches would have been more cold tolerant than their southern counterparts, but are expected to have had similar internal physiology, based on the similarity of egg morphology and Lower Pliocene skeletal remains (Lowe, 1931; Bibi et al., 2006). A sensitivity to the timing of seasonal precipitation is related to nutritional requirements associated with egg laying and would have been consistent between species. Unlike the fetus of modern northern arid-steppe and desert adapted herbivores, such as *Equus przewalski*, *E. hemionus*, *Camelus bactrianus*, and *Gazella subgutturosa*, ostrich eggs and hatchlings are less protected and highly susceptible to cold. The necessary combination of precipitation and warm temperatures would have made ostrich more vulnerable to increasingly cold winters and decreasing summer precipitation during the LGM and later Holocene.

Furthermore, atmospheric CO₂, which steadily rose following the LGM (Barnola et al., 1987), would have increased the productivity of C₃ grasses, but likely reduced digestibility in both C₃ and C₄ species (Morgan et al., 2004). The seasonal distribution of precipitation and temperature, especially mean temperature of the coldest month, are also important factors controlling plant primary production (Xiao et al., 1995; Xu et al., 2009). A cold dry climate with decreased summer precipitation, along with increased atmospheric CO₂, would have negatively impacted forage availability, and encouraged the spread of more drought resistant species of lower quality forage (Xiao et al., 1995).

Changes in the quality and productivity of forage in combination with a weakened summer monsoon during the LGM may have had severe repercussions for ostrich breeding and incubation. A more gradual and geographically variable deterioration in climate and forage during the Holocene could have a similar effect, contributing to the eventual demise of ostrich populations. Our youngest dates are from the western reaches of arid Northeast Asia and Holocene period archaeological sites in the more humid east rarely contain OES. The geographic-temporal distribution of our data suggest that East Asian ostriches were best suited to arid environments, as are African species. Early Holocene climatic amelioration throughout the northern and eastern regions would have gradually confined ostriches to more arid western deserts due to the encroachment of forest, forest-steppe and generally more humid steppe environments (Zhao et al., 2007; An et al., 2008). Rapid human population expansion into arid biomes may also have contributed to ostrich habitat constriction.

In the western Gobi Desert, there is a great deal of variation in local climatic regimes, but general trends suggest a dry Early Holocene, warm-wet middle Holocene, and widespread deterioration following 3 ka BP with weakening of the summer monsoon (Zhang et al., 2000; Zhao et al., 2007). Temperature steadily declined beginning about 5.3 ka BP (Zhang et al., 2000). Such an interplay may have created a more harsh environment for ostrich in North Asia, particularly if severe winter temperatures further limited annual grassland productivity. Further study of modern and palaeo-grasslands in the region and their response to external stimulus, including increased CO₂, changes in precipitation, and increased seasonality, will contribute to our understanding of East Asian ostrich palaeoecology and population dynamics.

6.2. Human expansion and ostrich interactions

Despite a lack of chronological control for post-LGM archaeological sites in northern China and Mongolia, the increased prevalence and density of microlithic sites, particularly in deserts and desert margins, is widely noted (Maringer, 1950; Chard, 1974; Bettinger et al., 1995; Janz, 2006; Barton et al., 2007). By the Early Holocene settled agricultural villages had emerged along the

Yellow River (Barton et al., 2009) and across the Loess Plateau, while highly mobile hunter-gatherers persisted throughout the more northern desert and steppe regions. Human occupation in ostrich habitat greatly increased through the terminal Pleistocene and Early Holocene.

Thus, the implication of humans in Asian ostrich extirpation seems reasonable. Increased human disturbance alone could have had indirect fitness costs on ostriches, which are sensitive to disturbance during breeding and nesting (Magige, 2008). Egg predation is expected because ostrich eggs each produce as much as 1.5 kg of protein and fat (Superchi et al., 2002), and egg clutches are sessile rather than mobile resources (Bird et al., 2009). These large birds themselves should rank high in human diets; *Struthio camelus* weigh between 130 and 160 kg and have up to 19% body fat carried external to muscle (Horbaniczuk et al., 2003). Nevertheless, while OES is common in North Asian archaeological sites, these sites contain no ostrich bones. This absence is true of ratites in general. They were hunted on other continents, but with few exceptions (giant flightless birds in Pleistocene Australia and recent New Zealand) ratite bones are rare in archaeological sites. Whether this is due to lack of hunting because of high cost due to extreme mobility (cf. Bird et al., 2009), or to taphonomic processes or butchering and transport techniques peculiar to ratites, remains to be determined (O'Connell, 2000). Nevertheless, it seems likely that human/ostrich interaction of some kind contributed to Asian ostrich extirpation.

6.3. Discussion

Mass extinctions occurred at a global scale during the Late Pleistocene, the process being most extensive in northern and mid-latitudes. Such regions are marked by both the simultaneous expansion of human populations and dramatic climate change, suggesting a correlation between the two (Barnosky et al., 2004). Similar evidence is attested to in the case of East Asian ostrich. Recent research in the ecology of catastrophic shifts in ecosystems draws attention to the importance of considering multiple stimuli in the ecological shifts that are related to extinction events (Scheffer et al., 2001). An ecosystem is vulnerable when various factors, such as changes in temperature and seasonality, precipitation and evaporation, habitat fragmentation or the invasion of a new predatory species, force that system to a critical limit. Changes in Pleistocene grassland vegetation and faunal composition represent a gradual, but ultimately catastrophic shift in northern and mid-latitude ecosystems.

Ostrich extinction in North Asia is seen as a symptom of both the restructuring of Pleistocene ecosystems through climate change, and the expansion of human populations. Changes in Pleistocene vegetation distributions and the inability of many large ungulates to adapt to climate driven changes and the loss of mosaic environments underlies ecological explanations for Late Pleistocene megafaunal extinctions in northern latitudes (Guthrie, 1984). Burgeoning populations of humans carrying increasingly efficient hunting technology are central to the “overkill” hypothesis (Barnosky et al., 2004). In this case, both factors are considered and would likely have contributed in varying degrees to ostrich extirpation. Environmental factors may have enhanced the vulnerability of that species, including increased seasonality and the spread of closed forest and forest–steppe vegetation at the loss of more arid desert steppes. At the same time, the demographic expansion of human predators could have further crippled restricted *Struthio* populations, ensuring the inability to adapt to climatic deterioration in the Mid- to Late Holocene.

7. Conclusions

Further study of OES from a range of localities and contexts are needed to accurately assess the cause of ostrich extinction in North Asia. Additional radiocarbon dates on both strictly palaeontological and as well as archaeological OES from across the region will clarify the ecological context of Late Pleistocene and Early Holocene ostrich home ranges. Trace element analysis might further reveal whether these and other specimens are exogenous to find locations and help reveal to what degree the seeming LGM reduction in ostrich abundance was accompanied by a reduction in total species range. The possibility that *Struthio* population expansion signals strengthening of the summer monsoons is worth further study.

We know the final extinction was in the Holocene, but not how long after our latest OES dates. As with the extinction of mammalian megafauna during the Pleistocene, the survivorship and extirpation of ostrich has important ecological and behavioural implications relating to humans. The OES associated with 11.1–6.9 ka BP TL-dated sediment at Yujiagou (Xia et al., 2001) is provocative, since the later ostrich survived in North Asia, the more likely it is they were affected by human intervention. *Struthio* remains do not occur in archaeological sites after the early Neolithic and probably did not survive past the Mid-Holocene as there is no clear historic documentation of ostrich in East Asia. As bovids came to dominate the arid steppes of northern Asia in the Holocene and cervids were highly successful in woodland and woodland–steppe environments (Guthrie, 1984), *Struthio* was apparently unsuccessful.

The relative roles of climate and human predation in ostrich extirpation are unclear. Progressively drier, cooler climates and the expansion of forests, humid steppe, and human predators might have all contributed to ostrich extinction. We can assume that Asian hunter-gatherers, like Africans, were ostrich egg predators (Sampson, 1994), and may have also hunted the birds though *Struthio* skeletal remains in Asian archaeological sites are non-existent. Even direct human disturbances, however, can indirectly affect ostrich fitness (Magige, 2008). If ostrich populations were eventually confined, along with other surviving large-bodied grazers (i.e., equids) to the desert and desert-steppe regions of Mongolia and northern China, where terminal Pleistocene and Early Holocene archaeological site density increased dramatically (Barton et al., 2007), ostriches may have found it increasingly difficult to survive interactions with burgeoning human populations. Such a range reduction could be demonstrated by more direct dates on OES.

While archaeologists seeking datable material in surface sites or sites containing no other datable material may be disappointed to realize that OES is sometimes older than archaeological deposits in which it occurs, such a date will at the very least provide an upper limit. The consistency of AMS dates from Shabarakh-usu suggests careful sampling may further alleviate the old-shell problem. Clearly, dating multiple OES from the same deposit, preferably in conjunction with AMS dates on charcoal or luminescence dates from associated sediments or pottery, will provide the best results and help clarify the dynamics of ostrich extinction, climate change and human interaction.

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